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The Planktonic Stages of the Haddock in Scottish Waters

By ALAN SAVILLE, B.Sc.

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MARINE RESEARCH

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The Planktonic Stages of the Haddock in Scottish Waters

By ALAN SAVILLE, B.Sc.

Marine Laboratory, Aberdeen

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The Planktonic Stages of the Haddock in Scottish Waters

INTRODUCTION

From its foundation the Marine Laboratory at Aberdeen has given haddock research a major role in its programmes. One of the more important results has been to demonstrate the part played by brood fluctuations in controlling the fortunes of the commercial haddock fishery of the North Sea. The work of Thompson (1930), Raitt (1939), Parrish (1949), and Jones (unpubl.) provides a measure of the size of each year brood since 1916, with the exception of some war years. The magnitudes of the fluctuations in brood strength over this period are shown in Fig. 1; they cover a range exceeding 50-fold.

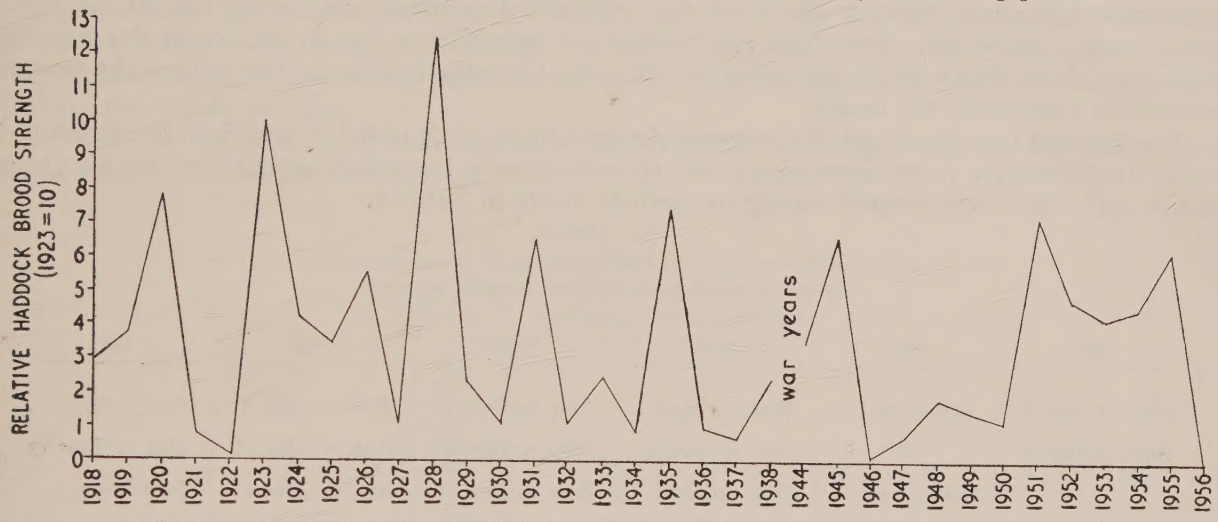

Fig. 1. Fluctuations in Haddock Brood Strengths in the North Sea, 1918-1956.

In a paper read before the Challenger Society in 1949 Parrish reviewed the possible causes of these fluctuations, and showed that they could not be related to the relevant fluctuations in the egg production potential of the spawning stock. He also demonstrated that no large-scale differential mortality occurred between the haddock assuming a demersal mode of life and their entry into the commercial catches. From these two results, he concluded that the factors determining the level of recruitment must be operative during the pelagic phase of the life history, between spawning and an age of about six months.

This paper by Parrish aroused considerable interest in the factors underlying the variations in recruitment. Previously Carruthers (1938) had found an inverse correlation between brood strength in east Anglian herring and that in haddock of the Northern North Sea and related these to fluctuations in wind strength and direction. Subsequently, Carruthers and his colleagues compared the brood variations in several fish with wind strengths and directions in various functions. In particular, Carruthers, Lawford, Veley and Parrish (1951) postulated a more precise correlation, for the years 1914-1948, between a certain wind function during the spawning period and the subsequent success of the haddock brood (see p. 16). These papers received criticism on purely statistical grounds by Gulland (1953). A correlation between offshore winds and brood strength for George's Bank haddock has also been demonstrated by Chase (1955). Rae (1957) discussed some of the implications and limitations of the haddock correlation of Carruthers and his co-workers, and linked the success of North Sea haddock broods with another wind function.

When the Carruthers' correlation was formulated knowledge of the planktonic stage of the haddock in Scottish waters was very slight. The approximate time and area of spawning were known from Thompson's work on the adult shoals but little or no direct work had been done on the egg and larval stages of the haddock since the classical researches of Schmidt (1909) and Damas (1909). In an attempt to fill this gap and in the hope that the knowledge so obtained would help to elucidate the haddock-wind

correlation, this laboratory began, in 1952, a series of cruises with the primary objective of investigating the pelagic phase of the haddock in the northern North Sea. Similar cruises were begun over the Faroe Plateau and have already been reported in part. This paper reviews the results of the North Sea investigation and their specific relevance to the postulated correlations between brood and wind.

MATERIAL

The haddock spawning in the North Sea cannot be considered as an isolated one. Schmidt (1909) showed that a considerable volume of spawning took place off the Scottish west and north coasts and it was realised that the products of this spawning might play a considerable part in recruitment to the North Sea. As it was not possible, however, to cover all this extensive area satisfactorily it was decided to concentrate the main effort in the North Sea. Additional sampling was carried out off the Scottish north coast as opportunity arose. This was neither as systematic as that in the North Sea nor did it always coincide in time with the sampling in that area. Accordingly it seems best to treat the two areas separately in considering the results.

The material from the North Sea covered the area from 57° N to 61° N and from the Scottish east coast to the Norwegian coast. Some ninety stations were more or less evenly spaced over this area to give a station grid which was sampled during the periods shown in Table I.

TABLE I

Periods in which North Sea was Sampled 1952–57

1952	1953	1954	1955	1956	1957
Mar. 21–Apr. 8	Apr. 3–20	Mar. 14–Apr. 1	Mar. 10–Apr. 7	Mar. 27–Apr. 17	Mar. 7–28
Apr. 23–May 7		Apr. 12–May 5	May 12–June 6	Apr. 21–May 15	May 31–June 13
	June 11–22	June 15–July 7	June 16–July 9	May 29–June 2	June 10–27

Off the north coast of Scotland the aim was to cover the area from the Butt of Lewis to Muckle Flugga (Shetland) lying within the 100 fathom contour. A grid of about forty stations was worked over this area during the periods shown in Table II.

TABLE II

Periods in which the North Coast Area was Sampled 1953–1956

1953	1954	1955	1956
Mar. 13–19	Apr. 23–27 June 13–18	Mar. 26–30 June 6–15 June 25–July 1	Apr. 9–23

In both areas samples were obtained by oblique hauls from bottom to surface with a 1 metre silk net of 60 threads per inch, towed at a speed of about 2 knots. The actual time the net was fishing was noted for each haul and after analysis the catches were converted to a standard 15 minute tow to make the hauls equivalent *inter se*. There was no sub-sampling in the laboratory, all eggs and larvae being extracted from the rest of the plankton, identified and counted.

SPAWNING SEASON

North Sea

Damas (1909) reviewed the findings of previous authors regarding the spawning time for haddock in the North Sea. He showed that the conclusion of Fulton (1905), that the haddock spawning

season in the North Sea extends from January to May, with February, March and April as the principal months, was in exact agreement with his own findings, based on the occurrence of eggs in the plankton. Thompson (1928), without quoting the basis for his statement, gave the haddock spawning season as January to May, with greatest intensity from mid-March to mid-April.

Because of the difficulty of separating the eggs of cod and haddock in their earliest stages (Saville 1956), newly spawned eggs cannot be used to delimit the spawning period reliably. Accordingly, it is preferable to use the earliest eggs which are definitely identifiable as haddock from the pigmentation of the developing embryo; this stage is attained when the eggs are about ten days old under the temperature conditions prevailing at that season.

No eggs in this stage of development have been taken, during the course of this investigation, in the North Sea in February. In all years in which the area was sampled, the first eggs which were definitely ascribable to haddock were sampled between the 7th March and the 11th March. This would place the beginning of spawning at about the 1st March. Eggs in this stage of development are also virtually absent from the collections after the last week of May, which infers that the spawning season ends about the middle of May.

In Table III are given the mean numbers of identifiable haddock eggs collected per haul in each fortnight throughout the period February to May.

TABLE III

Mean Number of Haddock Eggs per Haul in Fortnightly Periods

Date	Mean No. of Haddock Eggs
1—14/2	0
15—28/2	0
1—15/3	2·8
16—31/3	6·6
1—14/4	16·0
15—30/4	14·0
1—15/5	4·3
16—31/5	0·1

This table, bearing in mind that at the stage considered these eggs have a mean age of about 12 days, clearly shows that any spawning prior to the beginning of March, and after the middle of May, must be on a very small scale, whilst the peak of spawning takes place in the latter part of March and the first fortnight of April. There is no evidence of any significant variation in the spawning period between years.

North Coast

Sampling in this area was rather less satisfactory than in the North Sea, so that the spawning season can be traced with less confidence. The earliest identifiable haddock eggs were taken on the 24th February which would suggest that spawning in this area began about the middle of February. Eggs in this stage of development were still abundant at the end of April, but completely absent in June. As there was no sampling in May it can only be assumed that spawning finishes some time during that month.

It would appear, therefore, that spawning on the north Scottish coast begins rather earlier than in the North Sea and this conclusion is amply supported by the presence of distinctly larger larvae in the former area throughout March and April. It is of interest that Rae (1953) found for lemon sole a progression in the onset of the spawning season from the Scottish west coast, along the north coast and into the North Sea.

SPAWNING AREA

North Sea

Damas (1909) found that, although spawning was on a very small scale in coastal waters, beyond 40 metres' depth in the North Sea haddock eggs were taken in considerable numbers everywhere, with the

greatest concentrations in depths of more than 80 metres. Thompson (1928) delimited the spawning area from the distribution of large commercial catches of mature fish and concluded that haddock spawned in water of over 100 metres depth in the basin of the northern North Sea and the Gut.

In the present investigation the distribution of eggs up to the first appearance of the embryonic axis, i.e. eggs less than five days old, was used to get the best estimate of the spawning area. Within the area sampled eggs at this stage of development were found at almost every station except at those over the Norwegian Deeps, where they were absent. Within this area, however, some stations never provided more than very small numbers of eggs and can hardly be considered as centres of spawning; the few eggs taken there were probably dispersed from neighbouring spawning centres. Fig. 2 shows the area within which at some time during 1952-57 at least 50 eggs were taken at each station. For comparison the 16-egg contour is also shown and this extends the spawning area very little. The spawning area delimited in this way covers the whole of the northern North Sea from the Scottish coast to the Norwegian Deeps, with the exception of the Moray Firth and an area around the Fladen Ground. Apart from the absence of spawning over the Fladen area, this conclusion coincides closely with that arrived at by Thompson (1928) from the distribution of commercial catches. It is noteworthy, however, that Damas (1909) also commented on the scarcity of eggs in the Fladen area.

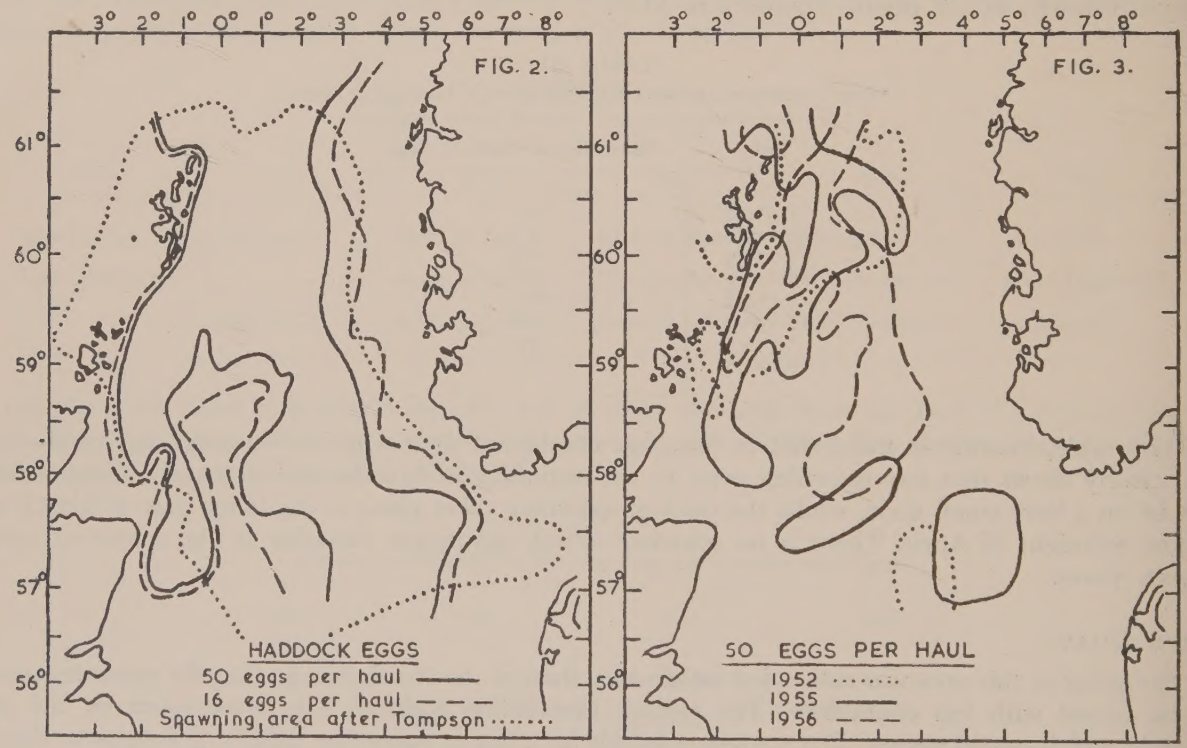

Fig. 2. Haddock Spawning Area in northern North Sea, 1952-1957.
Fig. 3. Haddock Spawning Areas in northern North Sea in individual years.

Although all of this extensive area has been used for spawning at some time during these years, in no individual year has spawning been so extensive and there has been considerable variation in the areas utilised in different years. In Fig. 3 are shown the 50-egg contours for three of these years to illustrate the extent of the variation between years. It will be noted that in 1956 the contour excluded most of the waters immediately to the east of Shetland, whereas in most other years these carried large populations of eggs, whilst in 1956 there was an unusual extension of high egg numbers over the banks bordering the western edge of the Norwegian Deeps. It seems noteworthy that the 1956 brood was unusually unsuccessful. The year 1955 was also noteworthy because of the absence of eggs immediately to the east of Shetland, but there was a band of high egg abundance across the mouth of the Moray Firth, while numbers in the east were relatively low.

Damas (1909) and Schmidt (1909) prescribed the physical condition suitable for haddock spawning as a salinity of 35·00–35·20‰ and a temperature of 5·5°–9·5°C. Conditions outside these values may well be limiting for reproduction in this species. Within the present North Sea surveys, however, values of temperature and salinity over the generalised spawning area were always within these ranges and the variations in the area used for spawning in different years do not appear to be controlled by either of these factors. Nor does the unsuitability of the Fladen as a spawning area appear to be associated with unsuitable temperature and salinity conditions.

Thompson (1928) stated that young haddock maturing for the first time within the Moray Firth do not move far to spawn, and he associated spawning across the eastern boundary of the Firth with a dense population of such haddock within it. Moreover, he showed that, east of 2°E, the spawning shoals tend to be mainly composed of older fish from the south and east of the North Sea. It would appear then that variations in the age composition and distribution of the adult shoals might control the variations in the favoured spawning localities between years. This is to some extent borne out by the data given for the abundance of different age groups of haddock in the Moray Firth by Jones and Main (1953, 1954, 1956), Jones (1957), Jones and Main (1958). Of the years considered in the present paper 1953 and 1954 carried much the heaviest stocks of first maturing spawners in the Moray Firth in the autumn. The years 1954 and 1955, according to the present data, were the two years when most spawning took place across the eastern boundary of the Moray Firth. No adequate data are available to investigate the relationship between easterly spawning and the distribution and abundance of older spawners.

North Coast

The only published work on the pelagic stages of the haddock to the north and west of the British Isles is that of Schmidt (1909); he found haddock larvae in this region in very great quantities everywhere within the 200 metre depth contour. Although Schmidt's data were collected only in May and June and refer only to larvae, the present more extensive data are in substantial agreement with his conclusions.

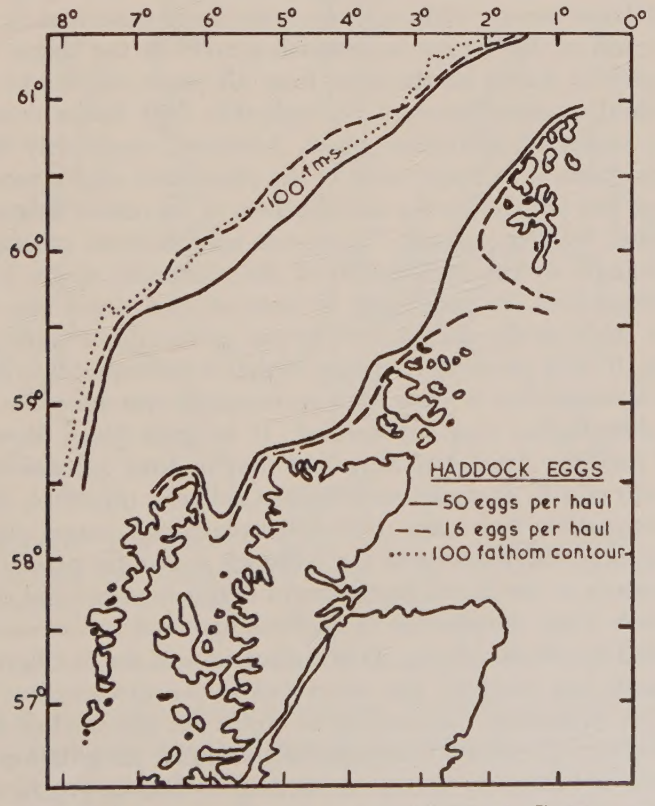

Fig. 4. Haddock Spawning Area on Scottish North Coast, 1953-1956.

Fig. 4 shows the distribution of early haddock eggs on the same basis as for the North Sea (Fig. 2). Spawning took place on a considerable scale over all the area between the 40 and 80 fathom contours to the north of Scotland. Unfortunately the data are completely inadequate to give any indication of the variation between years in the localities selected for spawning.

DISTRIBUTION OF LATE EGGS AND LARVAE

North Sea

At the outset of this investigation an assessment of the drift of the spawning products from the spawning centres was considered of great importance. The vital part which variations in speed and direction of drift might play in controlling brood fluctuations has been much stressed, for example by Damas (1909), Thompson (1922) and Carruthers, Lawford, Veley and Parrish (1951). The only previous work which attempted to trace the drift of the pelagic stages of the haddock in the North Sea was that of Damas (1909), who considered that normally the larvae were carried south towards the Dogger Bank, then east towards the Danish coast, ultimately tending north along the Norwegian Channel into the waters of the Norwegian Sea. Such a journey would demand either a very high rate of drift or a very prolonged planktonic life.

To measure the drift of the pelagic stages accurately entails a succession of cruises at close time intervals throughout the pelagic phase and an accurate measure of the rate of growth. Neither of these conditions was fulfilled in the present investigations. However, the available data are adequate to show any major transference of eggs or larvae within the sampled area. The distribution of those stations at which advanced eggs, small larvae and larger larvae were taken in number over the whole period of the investigation is shown in Fig. 5. A comparison of these distributions with that of recently spawned eggs (Fig. 2) would suggest that any drift was extremely slow and on too small a scale to play a significant part in affecting the subsequent size of the brood. The most significant change is to be seen between the distributions of small and large larvae. Although the main body continues to occupy the waters to the east of Shetland, to the south of this larvae were much scarcer in the larger sizes.

These figures are, however, based on the data from all years and might not show the effect of an exceptional year in which the normal pattern of negligible drift broke down. A comparison of the distribution of successive stages in individual years, however, completely bears out the conclusion arrived at from Fig. 5, that there is no major drift of the planktonic stages away from the area in which they are spawned. In Figs. 6-8 are shown the distributions of successive stages in the three years which give the best series of cruises for this purpose. There was no consistent pattern of movement in any of these years, any slight changes in the distribution of the successive stages being ascribable rather to dispersion than to directional drift. In particular, in none of these years was there any indication of a general movement of the main body of eggs and larvae eastwards towards and over the Norwegian Deeps. The year 1956 (Fig. 8) is of particular interest in that it subsequently yielded the poorest haddock brood on record. It is unfortunate that in June 1956 no sampling was done east of 2°E so that the eastern boundary of the larval distribution was not defined. It is quite clear, however, that there was no significant easterly trend between April and May and that in June a considerable body of larvae still occupied the same area west of 2°E. It would seem highly unlikely, therefore, that the failure of the 1956 year brood could be accounted for by a mass drift of the planktonic stages outwith the North Sea.

These relatively stationary distributions of the haddock spawning products may seem surprising if one thinks of water movements in the North Sea in terms of the conventional current picture as depicted by Tait (1937). An effectively static distribution of haddock eggs and larvae would seem more compatible with the theory propounded by Steele (1957). This author says of the northern North Sea:—"from this time onwards (March) until late autumn the water below the thermocline to the east of the prime meridian remains effectively stationary." According to Steele the thermocline is formed about mid-April and extends to a depth of about 30 metres. Unfortunately accurate information on the depth distribution of haddock eggs and larvae is extremely scanty. According to Damas (1909) the majority of the larval stages lie below 20 metres and thus it would appear that if one accepts Steele's interpretation the results

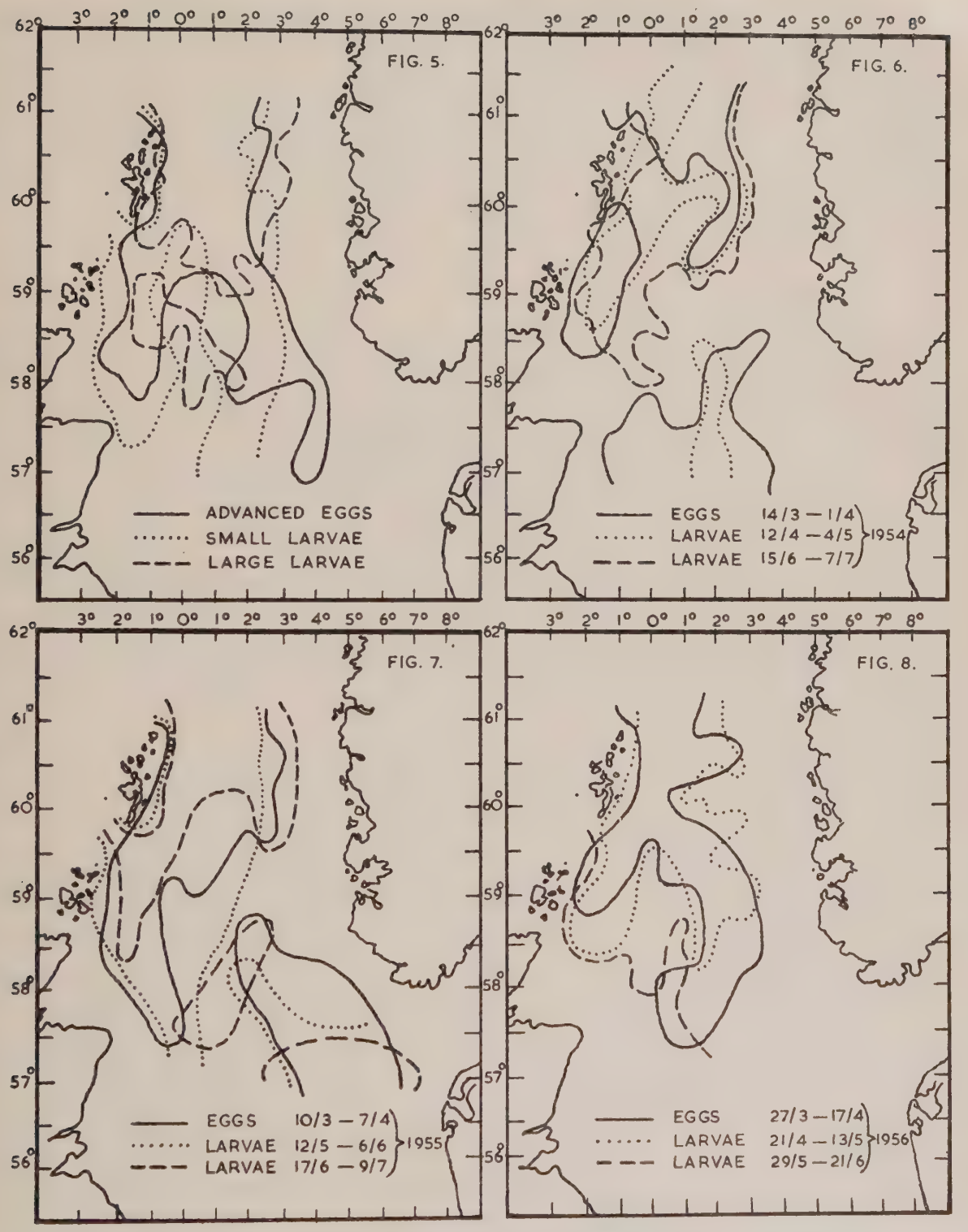

Fig. 5. Distribution of Haddock Eggs and Larvæ over all cruises in northern North Sea, 1952-1957.
Fig. 6. Distribution of Haddock Eggs and Larvæ on successive cruises in northern North Sea, in 1954.
Fig. 7. Distribution of Haddock Eggs and Larvæ on successive cruises in nothern North Sea in 1955.
Fig. 8. Distribution of Haddock Eggs and Larvæ on successive cruises in northern North Sea in 1956.

of this investigation are not incompatible with hydrographic findings. It is also worthy of note that, according to Steele, above the thermocline the most important influence is the westward spread of low salinity water originating in the Baltic outflow, a spread which may be stemmed but is never completely halted by wind stress. In the light of this it is difficult to conceive of any major loss of larvae due to easterly drift into the north-going stream along the Norwegian coast. To replace the intake of the Baltic current Steele also postulates a slow south-easterly drift of water off the Scottish coast. A result of this may perhaps be seen in the spread of larvae from the east of Orkney into the Fladen area apparent in the distributions of 1954 and 1955; although on the whole the later larvae appeared to be more restricted to the Northern waters than were the eggs.

North Coast

The importance of the grounds off the north Scottish coast as a spawning centre has been stressed by Schmidt (1909) and Thompson (1929). As pointed out by the latter author very few first or even second year haddock are to be found in this area so that the subsequent fate of the products of the spawning is of considerable interest. The part which this spawning may possibly play in recruiting to the North Sea was suggested in the Report of the Fisheries Board for Scotland (Anon. 1935), although Schmidt (1909) believed that they were transported to the Norwegian Sea and the North Sea. Schmidt's opinion was based on an analogy with the transport of salps in the North Atlantic Drift into these areas. This analogy would not seem to be a very sound one. The main path of the North Atlantic Drift is well offshore, beyond the continental slope, and hardly impinges at all on the coastal banks where the haddock spawn. The continental shelf to the north of Scotland has excited considerable hydrographic interest recently, more particularly in the part played by the passages between Orkney and Shetland as entrances for oceanic water to the North Sea (Tait 1930, Smed 1947, Fraser 1952, Craig and Lovegrove 1953). Such influxes in the spring and early summer could be expected to have a considerable influence on the fate of the planktonic haddock stages to the west of Orkney and Shetland. Fraser (1958) has also pointed out the possibility of the stock of haddock larvae in this area being augmented by larvae spawned on Rockall and Lousy Banks.

Consideration of Fig. 9, however, which shows the distribution of the successive stages throughout the period of the investigation does not add much support to the suggestion that this area plays an important part in recruiting to the North Sea. It will be seen that the general distribution on these grounds changed little from early eggs to advanced larvae. There was a slight tendency for a retreat of the eastern boundary westwards to the west of Orkney but no marked movement out of the area as a whole. There was no indication of the transport of eggs and larvae into the North Sea through the Orkney-Fair Isle passage although there was some indication of the passage of larvae through the Fair Isle-Shetland passage. It will also be noted that there was no evidence of any major loss westwards to the deep water beyond the continental shelf.

Unfortunately, only in 1954 and 1955 were there more than one cruise in a year from which to attempt to trace the distribution of successive stages and in these the cruises were too widely spaced to make this very profitable. They do, however, show some features which cast considerable doubt on the reality of the apparently static distributions shown in Fig. 9. The type of distribution shown in Fig. 9 for all stages, namely a continuous band from the Butt of Lewis to the west of Shetland is also typical for these stages in the individual cruises, with two exceptions. The June cruise in 1954 and the June-July cruise in 1955 show a rather different picture. In June 1954, Fig. 10, larvae were completely absent to the west of Shetland and indeed north of 59° 30′N. South of this a broad band of larvae to the north of Lewis and the Minch extended north-eastwards as two short tongues, one to the west of Sulisker Bank and the other to the east of North Rona. In June-July 1955, Fig. 12, on the other hand, larvae were practically absent south of 59° 30′N, the main body being concentrated to the west of Shetland. The exact significance of this is not clear, but the radical change in distribution and abundance in the last fortnight of June 1955 (Figs. 11 and 12) must cast considerable doubt on the apparent lack of drift in the combined data from all years. During both June 1955 and June-July 1955 the distribution of larvae to the west of Orkney and Shetland was continuous with that of the North Sea, both via the

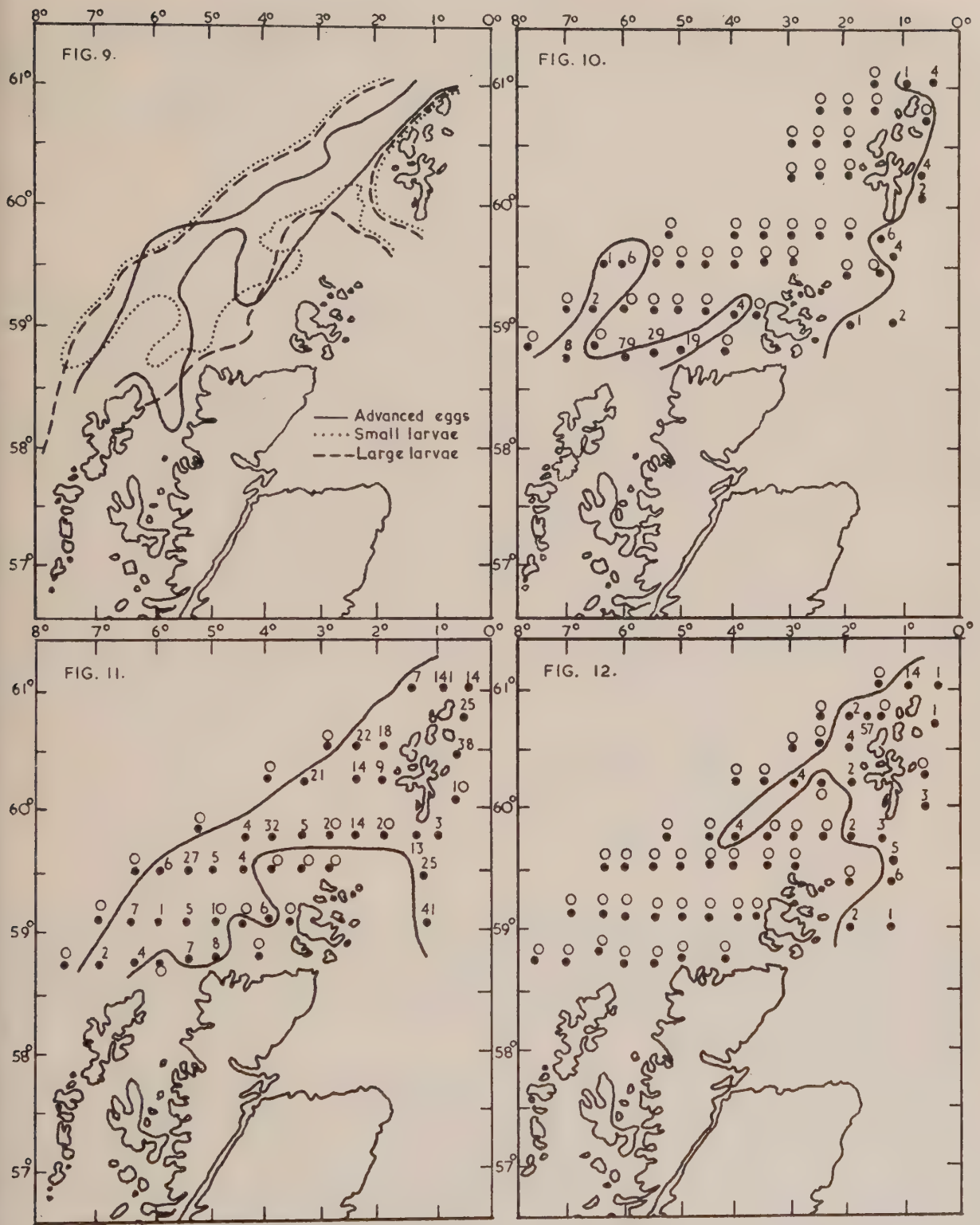

Fig. 9. Distribution of Haddock Eggs and Larvæ over all cruises on Scottish North Coast, 1953-1956.
Fig. 10. Distribution of Haddock Larvæ on Scottish North Coast in June, 1954.
Fig. 11. Distribution of Haddock Larvæ on Scottish North Coast in June, 1955.
Fig. 12. Distribution of Haddock Larvæ on Scottish North Coast in June-July, 1955.

Fair Isle-Shetland passage and via the north of Shetland, so that the possibility exists that the radical reduction in the numbers of larvae was due to a rapid and sudden drift through either of these entrances into the North Sea. Craig (1957) states that hydrographic evidence strongly suggests out-flow through the Fair Isle-Shetland passage in June 1955 which would make the latter route the more probable. On none of the cruises did the distributions suggest an influx through the Orkney-Fair Isle passage.

THE CRITICAL PERIOD

The third aim of the investigation was to test as far as possible Parrish's conclusion that the critical period occurred during the planktonic phase. Unfortunately, the cruises were not sufficiently frequent to permit mortality estimates being made between successive stages. All one can do is to estimate the mean numbers present on cruises which were completed and compare them with the subsequent assessment of the brood in its benthic phase. As the cruises in the different years were not strictly comparable in timing only major differences can be considered as significant. In Table IV are shown the mean number of early haddock eggs per haul in all cruises which adequately covered the spawning ground during the spawning season.

TABLE IV

Mean Number of Haddock Eggs per Haul 1952-1957

Cruise	Mean Number of Eggs
March 21–April 8, 1952	72
April 23–May 7, 1952	73
April 3–17, 1953	57
March 14–April 1, 1954	68
April 12–May 5, 1954	140
March 10–April 7, 1955	185
March 23–April 17, 1956	125
April 21–May 13, 1956	47
March 7–28, 1957	140

These figures would suggest that early eggs were considerably scarcer in 1952 and 1953 than in the other years which probably did not differ a great deal between themselves. Over these years the most striking difference in brood values is between the very poor brood year of 1956, when the numbers of eggs were fairly high, and 1952, which gave the best brood of these years and was probably the poorest year for eggs. Such discrepancies would not suggest that the success of a brood is determined by the numbers of fertilised eggs present.

The question whether the size of the brood is already fixed by the end of the planktonic stage is best tackled, with the present data, by considering the numbers of larvae present on the last cruise of each season and comparing these with the indices of abundance for the corresponding broods assessed in their second year of life. Unfortunately, the dates of the last cruises varied rather widely—with concomitant variations in the sizes of the larvae captured. Accordingly, it is not legitimate to compare numbers of larvae directly. To overcome this difficulty the numbers of larvae on each cruise have been converted to the equivalent numbers at an arbitrary size of 20 mm, by assuming that no differential mortality occurred thereafter. This technique does not measure whether the brood size was fixed by the end of the planktonic phase but rather whether it was already fixed by the time of the last cruise in which we sampled them in that particular year.

The figures derived in this way are shown in Table V.

TABLE V

Estimated Mean Number of Larvae on Last Cruise 1952–57

Year	Date of Last Cruise	Number of Larvae/ 10 hauls	Brood Index of 1+fish
1952	23/4— 7/5	26·0	147
1953	11—22/6	10·0	90
1954	15/6— 7/7	13·5	107
1955	17/6— 9/7	23·0	136
1956	29/5—21/6	14·0	2
1957	10/6—27/6	10·0	16

Although the larval numbers are obviously not proportional to those of the brood indices, with the exception of 1956 they do fall in the same order. These data, then, suggest that in normal years the fate of the brood is largely settled by about June and that differential mortality plays little part after that date.

The history of the 1956 brood is of peculiar interest as it was the only year of those considered which showed a really major deviation from the mean with regard to its brood index. Indeed 1956 provided the poorest brood since these records were begun with the brood of 1916. The larval values for 1956 and 1957 are probably rather biased upwards by all the sampling in the last cruises being confined to the west of 2°E—an area which normally carried the richer concentration of larvae. Moreover, in 1956 the assumption of a constant mortality on the larval stock found at the time of the last cruise probably was not sufficient. It is noteworthy that in that year the majority of the larvae found in June were unusually small and accordingly the cruise was less representative of the end of the pelagic phase. The level of mortality assumed to operate would then play a large part in controlling the final index. Table VI gives the abundance of the different haddock stages on the various cruises over the six years in which the North Sea had been sampled.

TABLE VI

Number of Various Stages per Haul on all Cruises 1952–57

Date of Cruise	Early Eggs Number per Haul	Advanced Eggs Number per Haul	Larvae Number per Haul
March 21–April 8, 1952	72	3	0·04
April 23–May 7, 1952	73	13	12·0
April 3-17, 1953	57	17	7·8
June 11–22, 1953	0	0	2·0
March 14–April 1, 1954	68	3·5	0·7
April 12–May 4, 1954	140	36	13·7
June 15–July 7, 1954	0	0	1·7
March 10–April 7, 1955	185	12	1·4
May 12–June 6, 1955	6	0·25	14·5
June 17–July 9, 1955	0	0	1·6
March 27–April 17, 1956	125	25	8·2
April 21–May 13, 1956	47	4	7·4
May 29–June 21, 1956	0	0	4·8
March 7–28, 1957	140	3	1·7
May 31–June 13, 1957	0	0	7·0
June 10–June 27, 1957	0	0	1·4

It will be appreciated that the timing of a cruise plays a major part in determining the abundance of any stage on that cruise. Accordingly, the abundance of a stage between years can only be compared on cruises which are fairly comparable in time. Table VI shows that on the first cruise in 1956 the numbers of all stages were well up to those obtained on comparable cruises in the other years. The second cruise of the year, which took place between 21st April and the 13th May, however, shows a rather different

picture. The numbers of early eggs on this cruise were much about the level to be expected in the light of the cruise timing. The numbers of late eggs and larvae were distinctly low. An examination of the size frequences of larvae on the relevant cruises would suggest that the deficiency in larvae on this cruise was only in respect of these of 6 mm and less, larger larvae were at least as abundant as in other years. On the last cruise, in June 1956, the mean number of haddock larvae per haul was again up to the level of comparable cruises in other years. It will be remembered (p. 8), however, that this estimate of abundance is biased in 1956 by the distribution of sampling. Moreover, Fig. 13, the size distribution of

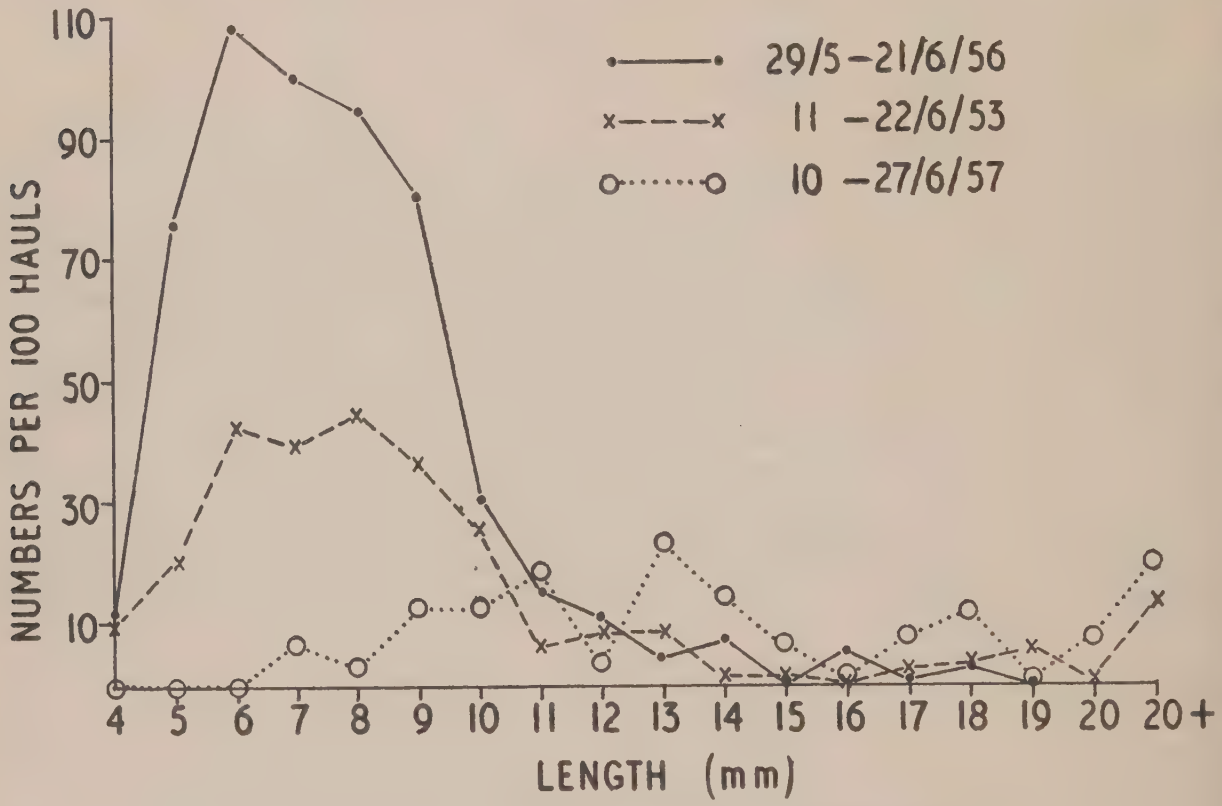

Fig. 13. Size Distribution of Haddock Larvæ in June, 1953, 1956 and 1957.

larvae captured on this cruise, in comparison with those of the larvae on comparable cruises in other years, shows that the high number of larvae on this cruise was almost entirely due to a preponderance of those less than 10 mm in length; above this size larvae were deficient in 1956 compared with the other two years and it will be noted that none at all were taken above a size of 18 mm. From such knowledge as we have of the growth of haddock larvae in other areas (Saville 1956) it can be expected that larvae of the size of 10 mm on this cruise would have been spawned about the last week of April. Those haddock spawned after this date would seem to have enjoyed favourable circumstances for survival—at least until the time when they were sampled in June; the June cruise, however, supplies further evidence of a heavy mortality affecting all those haddock spawned before the end of April. In view of the resultant low brood value a heavy mortality must also have occurred at some time after this date. Perhaps the most interesting conclusion to be drawn from this analysis is that the mortality in 1956 cannot be considered as having occurred solely at one critical phase in development, for example on hatching or at the transition from yolk-sac to active feeding. A similar conclusion was reached by Saville (1956) for the poor haddock brood of 1950 at Faroe. The data can be better explained by postulating a mortality affecting all stages present during one or more unfavourable periods, rather than as a continuous heavy drain affecting one stage of the development process. Marr (1956) in reviewing the literature bearing on mortality in the planktonic phase reaches a similar conclusion.

THE RELATIVE IMPORTANCE OF EGG AND LARVAL PRODUCTION OFF THE NORTH COAST AND IN THE NORTH SEA

The importance of the spawning region off the Scottish north coast was much stressed in the reports of the International Councils investigations in 1903-1906 on the biology of the gadoids. In the summary of the results (Anon. 1909) it is stated:—"haddock spawns in great quantity on the north and west coasts of Scotland and this is one of its richest spawning grounds." This statement is supported by d'Arcy Thompson (1909) who describes this region as yielding to Scottish fishermen the largest yield of haddock in the spring.

The results of the present investigation would not suggest that this region is of greater importance than the North Sea as a haddock spawning locality. In Table VII are given the mean numbers per haul of early eggs, of late eggs, and of larvae for the months of March, April and June for the two areas.

TABLE VII

Mean Catch per Haul of Haddock Stages in North Sea and North Coast

Month	Early Eggs		Advanced Eggs		Larvae	
	N. Sea	N. Coast	N. Sea	N. Coast	N. Sea	N. Coast
March . .	116	140	6·2	11·3	1·03	2·8
April . .	107	88	26	20·5	11	14·0
June . .	0	0	0	0	2·3	5·7

As regards early eggs the abundance is greatest on the North coast in March and in the North Sea in April, which again underlines the earlier spawning in the former region (p. 5), but over the season as a whole the values for the two regions are very similar. Moreover, the sampled area in the North Sea was about three times greater than that on the North coast with the result that the total production of eggs in the North Sea must have been considerably greater. It is possible, however, that the importance of the North Coast as a spawning centre has decreased since the time of these authors. D'Arcy Thompson (1909) showed clearly that at the time at which he wrote this area maintained a stock of larger haddock than did the North Sea, while Thompson (1928) showed that the older haddock of the North Sea move out to this region to spawn. Any tendency therefore to reduce the numbers of older haddock in the North Sea would presumably decrease the number available for spawning off the North Coast. Both Raitt (1939) and Russell (1939) demonstrated a marked reduction in the age and size composition of the haddock stock in the North Sea in the inter-war years, and Parrish and Jones (1953) have shown a recurrence of this feature in the post-war years. This reduction in the age composition of the haddock stock may well, therefore, account for the apparently reduced contemporary spawning on the North coast.

It is also instructive to compare the abundance of the later pelagic stages throughout the season in the two areas. The numbers of late eggs are also very similar for the two areas while, in the case of larvae, the numbers are somewhat though perhaps not significantly larger on the North coast. This situation would scarcely seem in support of the suggestion that the North Sea haddock stock is recruited in the planktonic stages by drift from the North coast. If this had been so one would expect the proportion of larvae to eggs to be higher in the North Sea. Indeed the figures would suggest that whatever the fate of the eggs spawned on the North coast the products of them are maintained in the area to quite a late planktonic stage. The ratios of the various stages in both areas are also very similar to those found for haddock at Faroe (Saville 1956), which can with some confidence be considered a self-contained stock.

THE CARRUTHERS WIND CORRELATION

The correlation between haddock brood strength and a wind function previously mentioned (p. 3) was the first of a series linking wind with recruitment in fish species (Carruthers, Lawford and Veley, 1951; Veley, 1951). The biological interpretation of some of the correlations has been attacked (e.g. by Graham, 1952), whilst the statistical basis of all of them was questioned by Gulland (1953). In their reply to these criticisms Carruthers, Lawford and Veley (1953) stated that they placed less importance on the interpretation advanced in explanation of their correlations than on their main thesis "that annual fish fortunes can hardly fail to be materially dependent upon these year from year differences in total commotion of the sea which can be attributed to the year from year differences in wind conditions which reigned during the individual spawning seasons." Apart from inherent probability the only support for this thesis rests on the correlations themselves and as the values prior to publication are open to the suspicion which attaches to all retrospective correlations, where there is considerable scope for the selection of one of the variables, one must judge the correlations and so the thesis on their success in prediction since publication.

It may therefore be apposite to review the present results in this light. The wind function used in the haddock correlation was $H = \sqrt{S^2+E^2} \sim \sqrt{N^2+W^2}$, the wind values being those of the period February-May. With this function high values could be due either to a dominance of NW or SE winds, while low values could be caused by either SW or NE winds although in practice they always proved to be due to the former. The analysis was carried further by considering the two cases of NW and SE winds separately, when it was shown that south-east winds were increasingly favourable with increasing wind values whilst NW winds were generally less favourable and gave a maximum recruitment at a value of about six. This situation was rationalised by assuming that spawning covered the period February-May and took place chiefly within the elliptical eddy system in the northern North Sea described by Tait (1937). North-westerly dispersion (due to south-east winds) was then assumed to distribute the spawning products over the main body of the North Sea and south-easterly dispersion within the eddy system unless the wind value was greater than six when they would be driven into the north-going stream along the Norwegian coast: a fate which would also befall larvae dispersed to the north-east under the influence of south-westerly wind.

This hypothesis fails to fit the facts brought out in the course of this investigation in several respects. The wind function used was based on wind values for the months of February-May: a period chosen on the basis of Thompson's assertion (1929) that spawning takes place during these months. Our data has shown that little or no spawning takes place in the North Sea in February and February winds can then have no direct effect on dispersal. On the other hand, the month of June when many planktonic larvae are still present is not included in the wind function. It would therefore appear that from the biological point of view the choice of wind data was not a particularly happy one.

The assumption that spawning largely takes place within the Great Northern Eddy would also seem to require some qualification. In all the years of this investigation some spawning took place in the general area which this system was depicted as occupying by Tait (1937). In none of them did the bulk of the spawning occur there and, as will be realised from the discussion of the spawning area, the proportion which did so varied considerably from year to year. Thus, even if the proportion of spawning which occurred in this area was large enough to have a critical effect on brood size, one would expect the reaction to wind influences to vary with the variations in spawning distribution as well as with wind direction and strength.

The crux of the biological interpretation of this wind correlation, however, is the assumption that the wind effect is through the dispersal of the spawning products. The demonstration from the present material that only minor movements take place during the planktonic stage would appear to undermine this. During the course of this sampling programme, over the period March-May when wind effect on transport would be expected to be most likely, the greatest variation in the easterly component was a mean value of $-2{\cdot}8$ for 1953 and of $-1{\cdot}0$ for 1954. If wind had an important effect on distribution in this area one would expect the larvae in June to have been more easterly in 1953 than in 1954. In fact the

reverse proved to be true. Indeed with the strongest component of westerly wind the June distribution of haddock larvae in 1953 showed the least extension to the east of any of the years sampled.

However, as pointed out previously, the vital test of the central thesis which underlies all the wind-brood correlations is the degree of success attained in predicting brood strength subsequent to the formulation of the correlation, when the dangers inherent in retrospection are no longer applicable. In this respect the haddock correlation is in some respect a key one in that it was the first produced, the success of which gave rise to further work. Moreover, it is the least suspect statistically because of the comparative straightforwardness of the relationship. The same wind function used by Carruthers and his collaborators has been calculated for the years subsequent to 1948 and plotted with the corresponding haddock indices in Fig. 14. It will be seen that, while the agreement between wind and brood

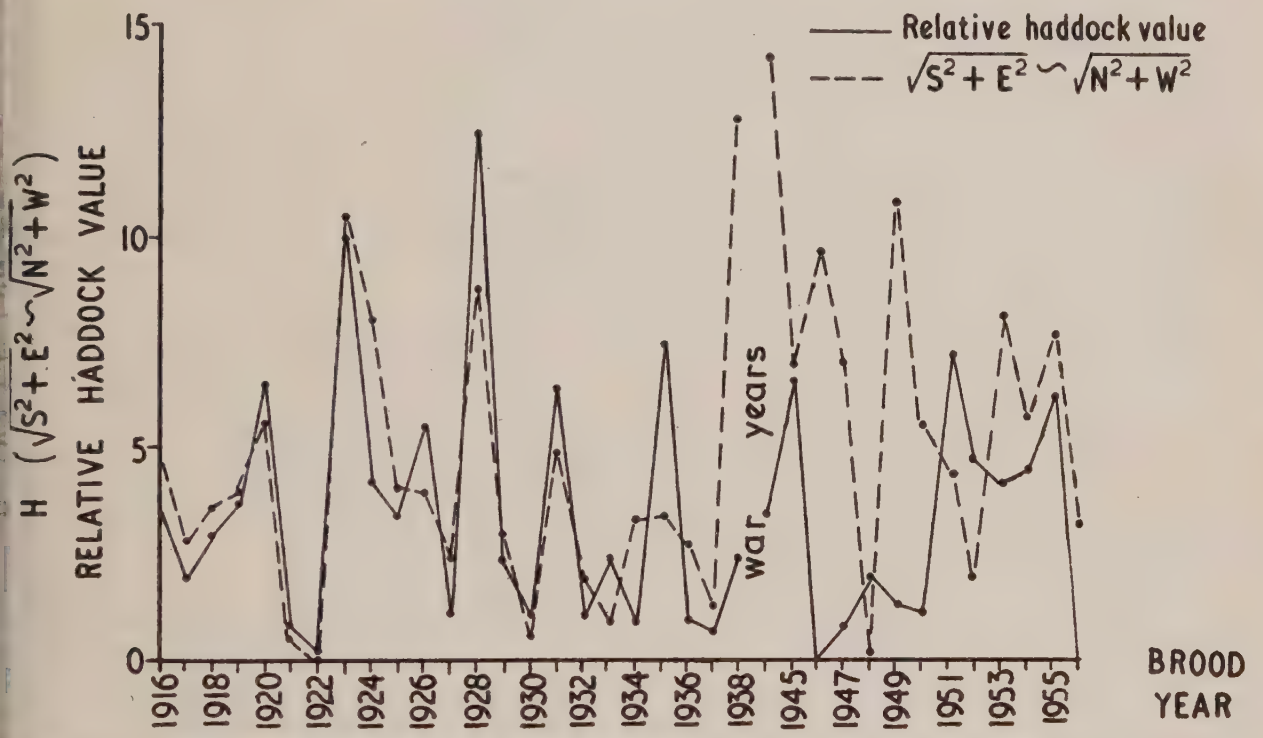

Fig. 14. The relative brood strengths of Haddock in the North Sea and the Carruthers Wind Function 1916-1956.

was very good until 1937, as pointed out by the authors the correlation was less satisfactory in the immediate post-war years. An analysis of the results in the period 1938-1957 shows no correlation between haddock brood size and the wind function used by Carruthers and his collaborators.

It is unfortunate that there are no comparable data on the pelagic stages of the haddock prior to 1938 when the Carruthers' wind function gave a satisfactory fit to the haddock index. It is possible that there has been a change in the ecology of the species during this period which has resulted in a breakdown of the correlation. In the period 1952-57, however, for which data on eggs and larval stages are available, this particular correlation with wind has failed and the history of the pelagic stages has been such that the mechanism suggested to explain it cannot be considered applicable.

Rae (1957) has recently proposed a relationship between wind and haddock brood strength on a rather different basis. He plotted the south-west component of the wind residual for the three months November-January against the size of the haddock brood spawned in the following spring. He found that all the above average broods were associated with lower wind values. Indeed Rae drew a well defined boundary at winds of about 250 miles per day above which good broods never occurred. A statistical analysis of this figure gave a probability of less than 0·002 of this distribution being fortuitous.

Re-examination of Rae's data has shown that, due to the use of faulty wind data for 1954 this slightly above average brood was placed in a wind category below 250 miles per day instead of above it. Recalculating the probabilities of Rae's contingency table to include this corrected datum and that now available for 1956 one gets a probability of 0·014 that the relationship is fortuitous. This—although much less convincing than the original figure—can still be accepted as significant.

Perhaps the most interesting part of Rae's paper, however, is his link between the same wind function and the distribution of *Metridia* at 10 m in the North Sea and his interpretation of the whole complex. The Rae wind-function is computed over the months November-January, i.e. previous to the actual spawning period. The effect on haddock survival must therefore be indirect and Rae suggests this effect is via the orientation of a favourable environment—for which *Metridia* is an indicator—over the spawning grounds. The distribution of *Metridia* at all depths has been plotted from the present samples for the cruises during which haddock spawning was in progress. The results suggest that this species is normally widely distributed over the spawning grounds during the spawning season. The only year of those for which we have data in which this was not true was in 1955 when *Metridia* was very scarce. As will be seen from Fig. 1, 1955 provided a good haddock brood. Moreover, 1956 yielded one of the poorest broods on record, yet there was then a general distribution of *Metridia* over the spawning area. Thus, while Rae's wind correlation may be valid and must be left to the judgment of time, it is evident that the presence or absence of *Metridia* alone is not a reliable indication of the suitability of the environment for haddock survival. The essentials of Rae's thesis, however, that it is the environment into which the eggs are spawned which governs survival, would appear to be supported by new data to be discussed later.

Glover (1958) mentions an interesting inverse relationship between haddock-brood strength and the fluctuations in the numbers of adult *Calanus finmarchicus* (Gunn.) in the northern North Sea. The interpretation of this correlation is not discussed and would seem difficult to reconcile with other data. The correlation itself, even in the ten years for which data are given, has certain unsatisfactory features. The *Calanus* values for the years 1952-54 are the highest of the years considered whilst the haddock broods of those years were considerably better than those of the period 1948-50 or of 1956. The correlation failed completely in 1957, since the *Calanus* figure for that year is easily the highest of the years considered, while the haddock brood value for 1957 is considerably better than the 1956 one.

We shall now look at some of the factors which might affect the survival of a brood. It was stated earlier (p. 6) that the area of spawning varies, within narrow limits, from year to year. As there is little evidence of any marked drift of spawning products, the water over the spawning locality selected has the greatest influence on the environment in which the larvae spend their planktonic existence, and it is only logical to look in the variations of this for a relationship with the subsequent brood indices. The greatest variation in spawning location is in the east-west axis and an examination of the distributions of early eggs in the various years did seem to suggest that the years in which spawning was farther east yielded poorer broods. To test this the proportion of the total spawning which took place east of 1°E was computed for the various years. The figures so derived are given, along with the corresponding brood index, in Table VIII.

TABLE VIII

Relationship between Easterly Spawning and Brood Index

Year	% of Spawning East of 1°E	Brood Index
1952	46·4	147
1953	50·6	90
1954	47·9	107
1955	46·2	136
1956	57·2	2
1957	52·6	16

While there is a suggestion here that the higher the proportion of spawning that takes place to the east the poorer the prospects for the brood, it is also quite clear that there is no direct proportionality about

it—the 1956 brood, for example, was very much poorer than can be accounted for by the somewhat higher proportion of easterly spawning. Nevertheless, the figures are suggestive of some sort of relationship between the two factors.

The outstanding variation in the post-war broods has been a series of poor broods from 1946-1950, of good-average broods from 1951-1955 and a return to a poor brood in 1956. Glover (1957), in discussing the planktonic environment of the herring in the northern North Sea over these years, remarks—"One might suggest that the period 1947-55 began with a typically neritic or North Sea type of environment and ended with a strong admixture of elements drawn from the water to the north of the Buchan fishing grounds. The increasing inflow of mixed water appeared to be most marked between 1951 and 1952, probably reached its maximum in 1953 and was maintained in 1954; but there may have been some reduction in 1955." In an addendum he remarks, "There was very little oceanic plankton in 1956." There are obvious parallels here with the variations in the haddock broods and one might form the hypothesis that poor broods are associated with neritic conditions in the North Sea. It is also noteworthy that 1953 and 1954 were the poorest of the post-war series of average-good broods and one might also wonder whether strongly oceanic conditions although not so deleterious as strongly neritic ones produce less good broods than mixed conditions.

Sagitta setosa J. Müller is generally considered as the best indicator of pure North Sea water (Fraser 1939). In 1956 this species was widely distributed over the Northern North Sea during the spawning period; in the other years of the period 1952-1957 it was rarely taken except at stations within the influence of the Baltic effluent over the Norwegian Deeps. An examination of the plankton records for the earlier post-war years also suggests it achieved a fairly wide distribution in the Northern North Sea during the spawning period in 1947 and 1948, both of which gave poor broods. Satisfactory data of plankton distributions in the Northern North Sea prior to 1936 are very scarce. It is of interest, however, that off the Northumbrian coast *S. setosa* was dominant in 1921 and 1922 while in 1923 and 1924 it was absent (Meek 1928). This is in close agreement with the present hypothesis. The years 1921 and 1922 were very poor brood years whilst 1923 and 1924 were well above average.

An examination of the plankton records, however, suggested that it was unlikely that all of the variability in haddock recruitment could be accounted for by variations in the extent of pure North Sea water and that oceanic influence also played its part. The planktonic indicators of oceanic influence in the Northern North Sea have been investigated by Fraser over a large number of years and a list of the more important indicators of this influx has been compiled (Fraser 1955). For the years 1936-57, exclusive of the war years, the distribution of these oceanic species and of *S. setosa* in the North Sea during the spawning period was plotted and the proportion of the spawning area which was free of either oceanic or neritic indicators was calculated as accurately as the data allowed. The results are given in Table IX together with the corresponding brood index.

TABLE IX

Distribution of Oceanic or Neritic Indicators over the Spawning Grounds

Year	% of Spawning Area Free of Oceanic or Neritic Indicators	Brood Index of 1 + Fish
1936	23	0·9
1937	23	0·7
1938	41	2·4
1947	24	0·7
1948	43	1·9
1949	27	1·4
1950	33	1·2
1951	87	7·3
1952	67	4·3
1953	53	4·2
1954	54	4·6
1955	89	6·3
1956	22	0·02
1957	37	0·2

It will be seen that in the really good brood years in this series—1951 and 1955—only about 10% of the spawning area was affected by oceanic or neritic indicators whilst in the poorest years such as 1936, 1937 and 1956 almost 80% was so affected.

There is, then, in these data, some evidence to suggest that the best haddock broods are produced in years when the plankton conditions over the spawning grounds during the spawning period are those characterised by Fraser (1939) as mixed oceanic-coastal. An unusual incidence of either oceanic or neritic elements seems to be inimical to the brood prospects. This conclusion is rather similar to that arrived at by Rae on different grounds. *Metridia lucens* Boeck can be considered as an indicator of mixed conditions in the Northern North Sea rather than of purely oceanic ones.

The generally favourable biological conditions produced by mixed oceanic-coastal water have been stressed by several authors. Russell (1939) has discussed the weakening of the Atlantic influence in the western Channel in the early nineteen-thirties. This was shown to be associated with a change from a predominance of *Sagitta elegans* Verrill to a predominance of *Sagitta setosa*, a drastic reduction in the overall abundance of fish larvae in the plankton and an almost complete cessation of recruitment to the Plymouth herring stock. Russell infers that the two latter effects were brought about by a scarcity of food induced in turn by the lower productive capacity of the water characterized by *S. setosa*. Fraser (1937, 1952), for the northern North Sea, associates mixed oceanic-coastal conditions with a richer crustaceous plankton than is to be found in either pure oceanic water or under purely coastal conditions. It might be assumed, therefore, that such mixed conditions would favour brood survival by providing richer conditions during the larval stages. The mathematical models of Beverton & Holt (1957) suggest that to account for the maintenance of stable fish populations it is necessary to assume that mortality in the larval stage is density dependent. Of the possible causes of a density dependent mortality rate competition for a limited food suply would seem the most likely.

The work of Wilson (1951) and Wilson and Armstrong (1952, 1954), moreover, suggests the further possibility that mixed oceanic-coastal water might contain some component favourable to egg development other than particulate food. Certainly the work of these authors related only to the eggs and larvae of a limited range of invertebrate material and it would be of great interest to attempt similar experiments with the eggs and larvae of fish. In the absence of evidence to the contrary, the possibility must be envisaged of waters of different types being of differing capacities in their ability to promote or inhibit the development of fish eggs and larvae. It might be thought that such an explanation is unlikely to account for the extreme type of mortality encountered in 1956 (p. 14), where apparently widely separated stages of development were affected. Such a possibility cannot be entirely neglected, however, as is shown by the wide range of effects of external metabolites discussed by Lucas (1947).

The present material is not suitable, and was not intended to discriminate between such alternative causes of brood fluctuations. The relationship suggested between brood size and the planktonic environment, if confirmed by future work, would however provide strong support for the hypothesis of Russell (1939) and Rae (1957) that such factors can play a major part in controlling brood survival. It is to be hoped that a realisation of the importance of such factors would in turn stimulate much needed research into the food requirements of fish larvae and their susceptibility to such features of their environment as external metabolites and growth promoting substances.

SUMMARY

The northern North Sea was extensively sampled during the planktonic phase of the haddock in each of the years 1952-1957 and the waters to the west of Orkney and Shetland in the years 1953-1956.

The spawning areas and the spawning season in the two regions are more accurately delineated than has been done previously. The subsequent distribution of eggs and larvae in the two areas and their inter-relationships are discussed. The conclusion is reached that drift during the planktonic phase is too slight to play a major role in controlling brood size.

Egg and larval abundance in the individual years are related to the subsequent success of the year

brood. It is concluded that variations in egg production do not have a decisive effect on brood size but that this is determined during the planktonic stage. The history of the poor 1956 brood during this stage is discussed.

Published correlations between haddock brood strength and environmental factors are reviewed in relation to the present material. It is shown that during the period of the present investigation there was some relation between brood strength and spawning locality and that over the period 1936-1957 brood strength correlated closely with the incidence of mixed oceanic-coastal conditions over the spawning area during the spawning season.

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